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Endogenous reserve dynamics of northern common eiders wintering in Greenland

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Abstract Endogenous reserves influence both survival and reproduction of many waterfowl species, but little is known about reserve levels of most species during the nonbreeding season, particularly those wintering at high latitudes. We investigated whether age, sex, and season were related to carcass composition of northern common eiders (*Somateria mollissima borealis*) wintering in southwest Greenland during 1999–2002. Adults carried more lipid and protein than juveniles during all winters. Among both age classes, males and females had similar fat levels but males carried slightly more protein. There was no dramatic seasonal variation in lipid or protein content. This suggests that during the period of this study, these eiders did not experience large-scale nutritional shortfalls. As predicted, Greenlandic eiders carried more lipid reserves than eider populations wintering in more temperate environments. Contrary to prediction, there was little relation between reserve levels and photoperiod, ambient temperature, or hunting disturbance intensity. Our results suggest that both sexes are

equally capable of dealing with nutritional deficits, and that juvenile birds are more prone to nutritional stress as evidenced by their consistently poorer body condition.

Introduction

Birds often experience energetic deficits, particularly during incubation, migration, or during severe weather events. Most store endogenous energy reserves to lower the risk of starvation during such periods. The primary endogenous reserve of birds is lipid (Griminger 1986), although protein can also be metabolized in times of severe nutritional stress (Blem 1990). Given the positive relationship often observed between endogenous reserve levels and survival, birds would be expected to carry the maximum amount of reserves possible. However, there are significant costs associated with carrying reserves. For example, heavy, less maneuverable birds may be at greater risk to both predation and injury during flight (Witter and Cuthill 1993). Thus, trade-offs exist between avoiding starvation while minimizing costs and risks associated with being fat (Lima 1986; Witter and Cuthill 1993).

Under situations where risk of starvation is relatively low, appropriate reserve levels may vary with factors affecting food availability and energy expenditure, such as weather, photoperiod, and hunting disturbance (Lima 1986; Blem 1990; Gaston 1991). For example, birds often store more reserves in response to shortened days (Blem 1990) and/or colder ambient temperatures (Gaston 1991). It has been suggested that this increase in reserves is in response to the heightened probability of encountering poor weather that would limit their ability to feed and increase their thermoregulatory costs (Lima 1986). Hunting disturbance may also affect the nutritional status of a bird because they expend energy trying to flee and the time they spend on predator avoidance may divert from time spent foraging (Bell and Owen 1990).

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Age may affect fat storing abilities, because young birds may have lower foraging efficiencies than adults (Goss-Custard and Dit Durell 1987). In addition to age, sex can potentially influence energy storing strategies. In winter, males tend to be heavier than females; however, once corrected for body size, most differences wane (Gauthier et al. 1992a; Hohman et al. 1992; but see Boos et al. 2002).

Among waterfowl, fat reserves are typically lowest following the breeding season, and then increase during fall to peak in early winter. Reserve levels subsequently decline throughout winter and increase again prior to and/or during spring migration (e.g., Peterson and Ellarson 1979; Gates et al. 2001). Similar seasonal patterns have been observed among captive waterfowl fed ad libitum (Williams and Kendeigh 1982; Barboza and Jorde 2002). Most studies of waterfowl endogenous reserve dynamics focus on herbivorous, migratory birds under temperate environmental conditions, and their results may under-represent the variation that actually exists in the wild. Therefore, there is continued need to study the endogenous reserve dynamics of species that vary in their migration, diet, and geographic range.

The Common Eider (*Somateria mollissima*) is a large diving duck associated with marine environments, which feeds primarily on benthic invertebrates (Goudie et al. 2000). Many populations winter at high latitudes (Goudie et al. 2000) and their annual survival and reproduction may be greatly influenced by food limitation in winter (Pehrsson 1984). Many eider populations declined in recent times (Goudie et al. 2000) and there have been numerous reports of large numbers of eiders starving to death during winter (Robertson and Gilchrist 1998; Camphuysen 2001). Despite this, little is known about their wintering physiology. Most studies of endogenous reserves of eiders have concentrated on the breeding season (e.g., Parker and Holm 1990; Hanssen et al. 2002). Only two studies have documented body condition dynamics of wintering common eiders and both were conducted in temperate regions (Scotland—Gorman and Milne 1971; United States—Korschgen 1977).

Here, we examine seasonal variation in endogenous reserves of northern common eiders (*S. m. borealis*) wintering in southwest Greenland. We initiated this study in order to establish baseline carcass composition data for eiders wintering at northern latitudes. Greenland holds an estimated winter population of 460,000 eiders (Merkel et al. 2002). Birds arrive from breeding grounds in eastern Arctic Canada and western Greenland in September–October and remain until April–May (Lyngs 2003). We predict that, once corrected for body size, males and females will have similar carcass composition and adults will have higher reserves than juveniles. We also predict that reserve levels will be related to (1) the risk of encountering poor environmental conditions that could increase their energetic requirements, and/or (2) factors that decrease their ability to feed. Specifically, we predict that birds should

maintain high fat reserves when temperatures are cold, days are short, and disturbance due to hunting is low. Finally, we discuss our results in relation to patterns reported among waterfowl wintering in more temperate environments.

Materials and methods

Collections

Seven hundred and forty-three common eiders were collected from the coastal waters ($n=485$) and fjords ($n=258$) of southwest Greenland as part of a legal subsistence harvest (Table 1). Birds were either shot or retrieved from fishnets where they were unintentionally drowned. In a previous study, we found no statistical difference between reserve levels of shot and drowned birds; therefore, we combined the samples (Merkel et al. 2006).

This study spanned three winters: 1999–2000, 2000–2001, and 2001–2002 (hereafter termed: 2000, 2001, and 2002, respectively). Eiders were collected from 1 November to 20 May. Throughout the study, early winter was defined as 1 November to 20 December, mid winter as 21 December to 8 February, late winter as 9 February to 31 March, and spring as 1 April to 20 May.

Carcass analysis

Ducks were sexed by syrinx morphology (Beer 1963). Birds were aged by plumage characteristics (Goudie et al. 2000), and length of the bursa of Fabricius (Mather and Esler 1999) and were categorized as follows: (1) adult—older than 3 years; (2) immature—2 or 3 years of age; and (3) juvenile—less than 1 year old. Immature eiders were rarely collected and were not included in this study.

The lengths of total head-bill, and the right tarsometatarsus bone were measured to the nearest 0.1 mm using calipers. Flattened wing length was measured to the nearest millimeter with a wing ruler. Birds were weighed to the nearest 1 g with an electronic scale. All drowned birds were scored for wetness. Correction figures of the amount of water retained within the feathers of drowned birds were obtained by weighing dried feathers of a sample of birds that had been plucked.

Breast muscles (both the pectoralis major and minor), leg muscles (all muscles that originate or insert in the femur or tibiotarsus bones), and leg fat pad were dissected from the right side of each bird and weighed. The abdominal fat pad was extracted and weighed. The gizzard muscle was excised, emptied, and weighed. All muscles and fat pads were weighed to the 0.1 g.

Proximate carcass analyses were conducted on a sub-sample of 92 birds. Data from these analyses were used to develop various predictive models using backwards stepwise multiple regressions (Jamieson et al. 2006). The

most accurate predictive models, as determined by their root-mean-square error (RMSE) of prediction, were selected. The RMSE and R^2_{adj} of the total lipid model are 14.60 and 0.93, respectively, and for the protein model the RMSE is 11.14 and the R^2_{adj} is 0.74. Age and sex class dummy variables were originally included in the models; however, they were removed because they did not significantly contribute to the models. These models were applied to the entire winter and spring sample to estimate their lipid and protein content. Models are listed below.

$$\begin{aligned} \text{Total lipid} = & -246.84 + 0.04 \text{ fresh body mass (g)} \\ & + 6.14 \text{ abdominal fat pad mass (g)} \\ & + 13.50 \text{ right leg fat pad mass (g)} \\ & + 0.90 \text{ flattened wing length (mm)}. \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Total protein} = & 73.92 + 0.08 \text{ fresh body mass (g)} \\ & + 0.82 \text{ right breast muscle mass (g)} \\ & + 0.52 \text{ gizzard muscle mass (g)} \\ & - 1.06 \text{ abdominal fat pad mass (g)}. \end{aligned} \quad (2)$$

Environmental data

Temperature and photoperiod during the study were gleaned from the Danish Meteorological Institute web site (www.dmi.dk). Harvest data were obtained from the Department of Fisheries and Hunting, Greenland Home Rule Government, Nuuk.

Statistical analysis

Principle component analysis was run on three measurements: total head-bill length, flattened wing length, and tarso-metatarsus bone length. The first principle component (PC1) was deemed to be an appropriate index of overall body size as all loadings were positive and ranged from 0.74 to 0.85, and PC1 explained 64% of the observed variance in the original variables. A general linear model was used to investigate body size variation among the various age-sex classes.

We examined the influence of season (four categories), sex (two categories), and age (two categories) on lipids and protein content of eiders, after controlling for body size with PC1 scores, using analysis of covariance (ANCOVA). In each analysis, all possible interactions were initially included. Interactions with $P > 0.05$ were removed sequentially according to P values (those with higher P values being removed first), and their sums of squares were combined with the sums of squares of the error term. The assumption of homogenous slopes was met, i.e., there were no significant interaction terms that included the covariate and any of the independent variables. Each year was analyzed separately because significant three-way interactions between year, season, and age were found when 2001 and 2002 were analyzed together. There were also empty cells in the first year of study. Post hoc comparisons of least mean squares were made with Tukey-Kramer pairwise tests. In all tests, the critical alpha was set at 0.05.

Table 1 Sample size, body mass, and carcass composition of northern common eiders collected in Greenland in relation to year, season, sex, and age

2000				2001				2002			
EW	MW	LW	SP	EW	MW	LW	SP	EW	MW	LW	SP
Sample size											
FAD 0	3	21	25	2	3	7	52	6	8	35	88
FHY 0	0	0	0	9	14	19	6	14	34	19	21
MAD 0	7	23	30	7	15	18	38	11	11	15	60
MHY 0	0	0	0	16	18	10	14	6	27	13	18
Body mass (g)											
FAD -	1,788 ± 103	1,937 ± 30	1,926 ± 35	1,916 ± 70	1,902 ± 85	1,847 ± 85	1,969 ± 22	2,085 ± 44	2,039 ± 64	2,024 ± 24	2,045 ± 15
FHY -	-	-	-	1,661 ± 40	1,726 ± 39	1,749 ± 38	1,615 ± 57	1,743 ± 36	1,843 ± 26	1,862 ± 30	1,765 ± 19
MAD -	2,136 ± 34	2,108 ± 31	2,107 ± 39	2,058 ± 32	2,092 ± 48	2,083 ± 46	2,041 ± 29	2,280 ± 41	2,293 ± 35	2,193 ± 51	2,237 ± 17
MHY -	-	-	-	1,787 ± 39	1,828 ± 28	1,725 ± 57	1,820 ± 49	2,033 ± 53	1,957 ± 27	2,065 ± 41	1,858 ± 37
Lipid content (g)											
FAD -	176 ± 6	202 ± 15	150 ± 11	153 ± 16	261 ± 3	169 ± 31	246 ± 13	237 ± 13	187 ± 27	194 ± 12	204 ± 8
FHY -	-	-	-	144 ± 24	150 ± 16	163 ± 15	101 ± 15	144 ± 17	183 ± 9	124 ± 8	94 ± 3
MAD -	194 ± 15	214 ± 18	196 ± 14	203 ± 27	311 ± 24	193 ± 11	215 ± 14	271 ± 23	230 ± 14	205 ± 19	226 ± 10
MHY -	-	-	-	154 ± 15	147 ± 8	124 ± 13	102 ± 9	206 ± 18	163 ± 7	145 ± 8	98 ± 5
Protein content (g)											
FAD -	375 ± 18	387 ± 4	387 ± 5	397 ± 6	395 ± 17	378 ± 7	386 ± 3	372 ± 29	372 ± 21	390 ± 6	398 ± 2
FHY -	-	-	-	339 ± 8	363 ± 7	359 ± 5	345 ± 8	354 ± 5	365 ± 4	374 ± 4	370 ± 3
MAD -	430 ± 8	420 ± 5	412 ± 6	417 ± 8	410 ± 5	416 ± 6	405 ± 8	430 ± 6	438 ± 6	426 ± 7	433 ± 3
MHY -	-	-	-	367 ± 6	379 ± 5	366 ± 8	379 ± 8	394 ± 8	392 ± 5	407 ± 6	389 ± 2

Notes: EW = early winter (01 Nov–20 Dec); MW = mid winter (21 Dec–8 Feb); LW = late winter (9 Feb–31 Mar); SP = spring (1 Apr–20 May); F = female; M = male; AD = older than 3 years; HY = younger than 1 year
Means ± SE are presented

Relationships between monthly mean fat reserve mass of each age-sex class and monthly mean ambient temperature, photoperiod, and harvest disturbance (indexed by the number of harvested eiders reported in Nuuk) were investigated using Pearson's correlations. *P*-values were adjusted using the Bonferroni method. Only birds collected in the coastal waters were included in this analysis (adult females $n=117$; juvenile females $n=136$; adult males $n=124$; juvenile males $n=108$). We chose not to include birds collected in the fjords because they are not heavily hunted by people (Merkel 2004) and it appears that they feed nocturnally due to heavy predation by White-tailed Eagle (*Haliaeetus albicilla*; F.R. Merkel and A. Mosbech, personal communication). These two factors added much noise to the analysis although the overall results were the same whether or not fjord birds were included. All statistical analyses were carried out using SYSTAT 9 (SYSTAT Software Inc. 1999).

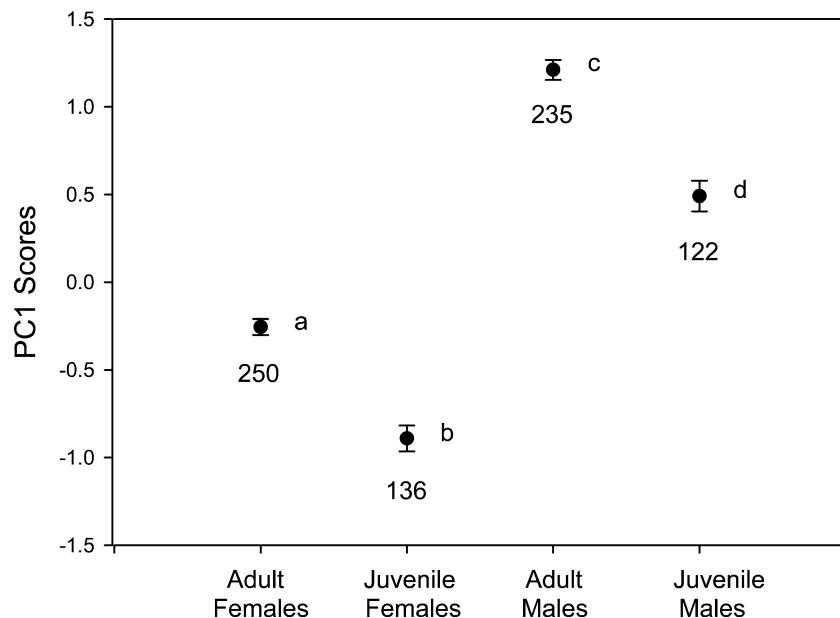
Results

Effects of age and sex on body size and endogenous reserves

Males were larger than females and adults were larger than juveniles (Fig. 1). In all analyzes of protein, no interactions were found to be significant (Table 2). In the lipid analyses, there were significant interactions between age and collection period in 2001 and 2002; the 2 years when both age-classes were collected (Table 2).

In every collection period, adults were fatter than juveniles (Table 3), although in 2001 differences were not significant in early and late winter and in 2002 differences were not significant in mid winter (Table 3). In both 2001 and 2002, adult eiders carried significantly more protein than juveniles (Table 4).

Fig. 1 Body size (represented by PC1 scores of total head-bill length, flattened wing length, and tarso-metatarsus bone length) of northern common eiders in relation to age and sex. Numbers associated with standard error bars represent sample sizes. Comparisons were made with a general linear model and plots with different letters are significantly different ($P<0.05$)



Sex did not interact significantly with any other variable (Table 2). There were no significant differences between the amount of lipid stored by males and females (Table 5). Males consistently carried more protein than females, although this difference was significant only in the third year of study (Table 5).

Effect of season on endogenous reserves

The pattern of carcass lipid differed between years and age classes (Table 1—raw data; Table 3—least mean squares data). In 2000, there were no significant seasonal differences in the lipid levels stored by adults (ANCOVA; $P>0.05$; Table 4). However, in 2001, adults stored significantly more fat in mid winter than they did at any other time (Table 3). In the same year, there was no significant variation in lipids stored by juveniles (ANCOVA; $P>0.05$; Table 3). In the winter of 2002, there was no significant seasonal variation in the amount of fat carried by adults (ANCOVA; $P>0.05$; Table 3). However, lipid levels of juveniles were constant from early to mid winter but then tended to decline by spring (Table 3).

In all three winters, carcass protein did not vary significantly among seasons (ANCOVA; $P>0.05$; Table 1—raw data; Table 6—least mean squares data).

Seasonal patterns of temperature, day length, and hunting disturbance

If eiders stored reserves to buffer against the lowest ambient temperatures of the winter (Fig. 2a), then reserves of Greenlandic eiders should rise from early winter to mid winter then remain stable through late winter to decline in spring. This pattern was not

Table 2 The influence of sex (female, male), age (adult, juvenile), and season (early, mid or late winter or spring) on carcass composition of common eiders wintering in Greenland

Year ^a	Carcass component					
	Lipid			Protein		
	df	F	P	df	F	P
2000 ^b						
Sex	1	0.35	0.56	1	1.84	0.58
Season	2	1.85	0.16	2	0.55	0.18
PC1 ^c	1	5.94	0.02	1	46.79	<0.001
Error	95			94		
2001						
Sex	1	3.55	0.06	1	1.67	0.20
Age	1	40.46	<0.001	1	50.65	<0.001
Season	3	7.25	<0.001	3	1.01	0.39
PC1	1	4.07	0.05	1	59.12	<0.001
Age × season ^d	3	8.81	<0.001	—	—	NS
Error	225			228		
2002						
Sex	1	2.48	0.12	1	24.29	<0.001
Age	1	75.90	<0.001	1	106.81	<0.001
Season	3	13.48	<0.001	3	1.41	0.24
PC1	1	25.46	<0.001	1	134.90	<0.001
Age × season	3	6.65	<0.001	—	—	NS
Error	366			367		

^aEach year was analyzed separately because there was a significant three-way interaction (year × season × age) when 2001 and 2002 were analyzed together

^bIn 2000 only adults were collected, so age was not included as a variable

^cPC1 of the lengths of flattened wing, tarso-metatarsus bone, and total head, was included as a covariate to adjust for body size, see **Materials and methods section**

^dInteractions are reported only if they were significant

observed in any of the age–sex classes (Table 1), and there were no significant correlations between the amount of fat stored by any of the age–sex classes and the monthly mean temperatures (adult females—Pearson's $r = -0.40$, $P = 1.00$, $n = 16$; juvenile females—Pearson's $r = -0.48$, $P = 1.00$, $n = 15$; adult males—Pearson's $r = -0.26$, $P = 1.00$, $n = 16$; juvenile males—Pearson's $r = -0.54$, $P = 1.00$, $n = 13$).

If eiders store reserves to buffer the effects of short days or are limited by hunting disturbance, then reserves

should be highest in early and mid winter then decline steadily throughout late winter and spring (Fig. 2b, c). To some degree, this pattern was observed in the lipid dynamics observed in juveniles, particularly males (Table 1). However, when the data were analyzed with Pearson's correlations the only significant relationship found was between juvenile male lipid levels and hours of daylight (adult females—Pearson's $r = -0.23$, $P = 1.00$, $n = 16$; juvenile females—Pearson's $r = -0.41$, $P = 1.00$, $n = 15$; adult males—Pearson's $r = -0.64$,

Table 3 Analysis of carcass fat of common eiders collected in Greenland in relation to age and season

Year ^a	Age class	Season					
		Early winter lipid (g)	P	Mid winter lipid (g)	P	Late winter lipid (g)	P
2000 ^b	Adults	—	—	184.2 ± 22.8 (10)	0.70	204.4 ± 10.8 (44)	0.14
2001	Adults	180.1 ± 25.6 (9)	<0.01	305.3 ± 17.7 (18)	<0.001	181.7 ± 15.1 (25)	0.09
	P	1.00		<0.001		0.89	<0.001
2002	Juveniles	161.0 ± 16.2 (25)	1.00	150.3 ± 13.6 (32)	1.00	153.5 ± 14.0 (29)	0.48
	Adults	250.0 ± 14.5 (17)	0.47	210.7 ± 13.3 (19)	0.99	198.1 ± 8.2 (50)	0.94
	P	0.01		0.56		<0.001	<0.001
	Juveniles	178.9 ± 12.9 (20)	1.00	181.5 ± 7.4 (61)	0.01	135.2 ± 10.0 (32)	0.22
							101.8 ± 9.2 (39)

Presented are the probabilities from Tukey–Kramer pairwise tests that adjacent means within a row or a column are significantly different. Presented are least mean squares (LMS) of lipid content resulting from the following ANCOVA: lipid = PC1 + sex + age + season + age × season, where PC1 was included as a covariate to adjust for body size

^aYear was a confounding variable, so each year was analyzed separately

^bIn 2000 only adults were collected. No collections occurred in early winter

Table 4 Protein content in relation to age among northern common eiders wintering in Greenland

Year ^{a, b}	Age class	Protein content (g)	<i>P</i> ^c
2001	Adults	395.2 ± 2.2 (142)	< 0.001
	Juveniles	371.8 ± 2.2 (106)	
2002	Adults	407.6 ± 1.6 (234)	< 0.001
	Juveniles	384.3 ± 1.6 (152)	

Least mean squares of protein content resulting from the following ANCOVA: protein = PC1 + sex + age + season, where the covariate, PC1, was included to adjust for differences in body size

^aYear was a confounding variable, so each year was analyzed separately

^bIn 2000 only adults were collected, therefore it was not analyzed for age differences

^cThe probability from ANCOVA

$P=0.14$, $n=16$; juvenile males—Pearson's $r = -0.79$, $P=0.03$, $n=13$). There were no significant relationships between lipid levels and hunting disturbance (adult females—Pearson's $r = -0.46$, $P=1.00$, $n=16$; juvenile females—Pearson's $r = -0.01$, $P=1.00$, $n=15$; adult males—Pearson's $r = -0.39$, $P=1.00$, $n=16$; juvenile males—Pearson's $r = -0.72$, $P=0.10$, $n=13$). It should be noted that, due to changes in hunting regulations, the number of eiders hunted in 2002 was well below the normal mean harvest levels. If lipid dynamics were strongly influenced by hunting disturbance you would expect lipid levels in 2002 to reflect this change; however, there was no corresponding change in lipid dynamics.

Discussion

Endogenous reserve levels of birds are dynamic and influenced by both internal (e.g., breeding status) and external factors (e.g., social status, environmental conditions). Among temperate waterfowl fat reserves are typically lowest following the breeding season, and then increase during fall to peak in early winter. Reserve levels subsequently decline throughout the winter and increase again prior to and/or during spring migration (e.g., Peterson and Ellarson 1979; Gates et al. 2001). This general pattern was not observed in our study, suggesting that Northern Eiders are influenced by some factors other than those affecting temperate waterfowl populations.

Effects of age and sex

Male common eiders were significantly larger in body size than females (Fig. 1), but no significant difference in lipids was found between the sexes once data were adjusted for body size (Table 5) similar to findings of Gauthier et al. (1992a) and Hohman et al. (1992). This suggests that male and female eiders are equally capable of dealing with nutritional deficits. Eiders forage in large

mixed flocks and do not defend individual feeding territories; therefore, being larger may not necessarily put males at a competitive advantage.

After controlling for structural body size, male carcasses contained more protein than female carcasses in winter across all 3 years, albeit the differences were small and statistically significant in only 2002 (Table 5). There could be several possible advantages for adult males to maintain greater protein mass. Males with more protein, and hence muscle, may be superior at protecting females from interruptions during pre-breeding hyperphagia (Hepp 1984; Rohwer and Anderson 1988). These males may also be most effective at acquiring mates and defending them against extra-pair copulations (Patten-
den and Boag 1989). Among Cinnamon Teal (*Anas cyanoptera*) the protein content of males was positively related to pair formation and duration, whereas body size and lipid content were not (Hohman and Ankney 1994). These issues may be particularly important among common eiders where males often outnumber females in early spring (Gaston and Cooch 1984) and near breeding colonies (Christensen 2000). Eiders pair in early winter (at least in Scotland, Spurr and Milne 1976), and the result that male northern common eiders maintain high protein levels throughout the nonbreeding period (Table 1) suggests that they may also pair before spring migration, although this remains unknown in Greenland.

Adult eiders were structurally larger than juveniles (Fig. 1), and adults carried more protein (Table 4) and lipids than juveniles, although these latter differences were not always significant (Table 3). These differences in carcass composition suggest that juveniles are more prone to nutritional stress than adults. This supports field observations that juvenile eiders succumb first during large-scale die-off events (Camphuysen 2001; S.E. Jamieson unpublished data). In waterfowl, it is common for adults to have higher body condition than juveniles of the same sex (Peterson and Ellarson 1979; Kestenholz 1994). A lower body condition may reflect that juveniles have lower foraging efficiency due to inexperience, interference competition with adults, or both (Goss-Custard and Dit Durell 1987). However, a study on common eiders in Newfoundland found no apparent difference in foraging efficiencies of immature and adult males (MacCharles 1997).

The size disparity between adults and juveniles may also have promoted differences in endogenous reserve levels. The size difference observed between the two age-classes indicates that juvenile eiders are still growing in their first winter. Consequently, they may not be able to store as much lipids and protein as adults because they are continuing to invest energy in growth. Also, smaller birds have higher mass-specific metabolic rates (Kend-
eigh 1970), suggesting that juveniles must use more energy per unit mass for maintenance. Both factors, which are not mutually exclusive, might constrain their ability to accumulate fat in winter.

Table 5 Carcass composition in relation to sex among northern common eiders wintering in Greenland

Year ^a	Sex	Lipid content (g)	P ^b	Protein content (g)	P
2000 ^c	Females	183.4 ± 13.5 (49)	0.56	401.3 ± 4.3 (49)	0.58
	Males	193.6 ± 11.4 (60)		408.7 ± 3.6 (60)	
2001	Females	195.9 ± 9.5 (112)	0.06	381.2 ± 2.5 (112)	0.20
	Males	172.0 ± 7.7 (136)		385.7 ± 2.1 (136)	
2002	Females	189.4 ± 5.1 (225)	0.12	389.6 ± 1.6 (225)	< 0.001
	Males	176.9 ± 5.7 (161)		402.3 ± 1.6 (161)	

Least mean squares of lipid content resulting from the following ANCOVA: lipid = PC1 + sex + age + season + season × age, where PC1 was included as a covariate to adjust for body size

Least mean squares of protein content resulting from the following ANCOVA: protein = PC1 + sex + age + season, where the covariate, PC1, was included to adjust for differences in body size

^aYear was a confounding variable, so each year was analyzed separately

^bThe probability from ANCOVA

^cIn 2000 only adults were collected; therefore age was not included as an independent factor

Seasonal dynamics of carcass composition in winter

As expected, there was very little variation in protein content of eiders collected in Greenland either during a winter or across years (Table. 1, 6). Uniformity in protein content throughout the nonbreeding season has been found previously among eiders (Gorman and Milne 1971), and other species of waterfowl (Gauthier et al. 1992b; Boos et al. 2002). Protein is normally not metabolized as an energy source unless the individual is under extreme nutritional stress (Blem 1990). Therefore, the observed constancy in protein levels of eiders suggests that during the three winters of this study, eiders did not face any prolonged energetic shortfalls. However, it should be noted that eiders experiencing extreme nutritional stress may not have been collected by us if they died naturally, or if they recovered between our sampling periods of several weeks (see **Materials and methods** section).

Although the endogenous reserve pattern found in many temperate waterfowl populations was not observed, there was variation in the amount of fat stored throughout the nonbreeding season but it varied annually and between the age and sex classes. Juvenile fat levels, however, declined every year towards spring. In the spring sample we included a large number of birds collected in the fjords which are heavily depredated by White-tailed Eagles (F.R. Merkel and A. Mosbech,

personal communication). It is possible that the juveniles are unable to compensate for this predation pressure and thus utilize their fat stores. More likely, however, is that lipid reserve levels in juveniles decrease during late winter and spring because the probability of encountering severe weather during this period is also declining.

Although there was a weak tendency for lipids to be higher in mid winter, overall there was little variation in lipids throughout the winter (Table. 1, 3), similar to other eider populations (Milne 1976; Korschgen 1977). This suggests that they typically have access to reliable food resources in winter.

The influence of environmental conditions on endogenous reserve dynamics

External factors, both natural and human induced, can influence how and when birds store reserves. Fat levels often increase in relation to decreasing day length (Blem 1990), increasing latitude (Rogers et al. 1993), and decreasing ambient temperature (Gaston 1991), although it is often difficult to differentiate among these factors.

If current ambient temperature had a strong influence on how eider ducks acquired lipids, then the lipid dynamics in all three winters should be similar because

Table 6 Protein content in relation to season among northern common eiders wintering in Greenland

Year ^a	Season						
	Early winter protein (g)	P	Mid winter protein (g)	P	Late winter protein (g)	P	Spring protein (g)
2000 ^b	—	—	409.0 ± 7.2 (10)	0.83	404.4 ± 3.4 (44)	0.71	401.5 ± 3.1 (55)
2001	381.0 ± 3.8 (34)	0.51	387.6 ± 3.0 (50)	0.79	383.8 ± 2.8 (54)	0.93	381.6 ± 2.2 (110)
2002	391.6 ± 3.1 (37)	0.51	396.8 ± 2.1 (80)	1.00	396.8 ± 2.0 (82)	0.87	398.6 ± 1.5 (187)

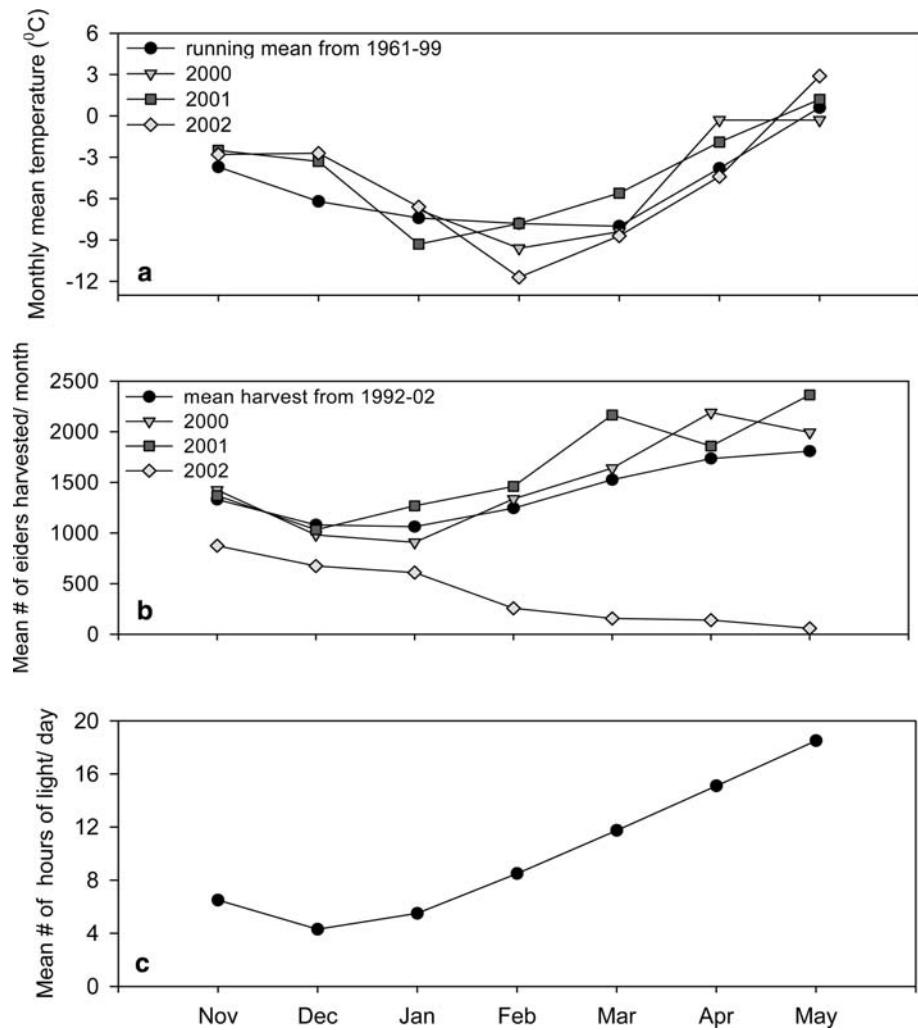
Presented are the probabilities from Tukey-Kramer pairwise tests that adjacent means are significantly different

Least mean squares of protein content resulting from the following ANCOVA: protein = PC1 + sex + age + season, where the covariate, PC1, was included to adjust for differences in body size

^aYear was a confounding variable, so each year was analyzed separately

^bIn 2000 only adults were collected. No collections occurred in early winter

Fig. 2 Ambient temperature, hunting intensity, and photoperiod in the Nuuk region, southwest Greenland



monthly mean temperatures did not vary much between years (Fig. 2a). However, lipid dynamics of eiders did not mimic the temperature dynamics (Table 1).

The low thermal conductance of eiders (Jenssen et al. 1989) may explain the poor relationship between the dynamics of ambient temperatures and lipids. It is also possible that the eiders adjusted their behavior in response to the colder temperatures and these behaviors masked any effect that temperature may have had on lipid levels; such behavioral flexibility has been documented in other waterfowl. For example, Mallards (*Anas platyrhynchos*) faced with a drop in ambient temperature decreased their activities; particularly non-essential, energetically expensive ones (Jorde et al. 1984). Systad and Bustnes (2001) found that in colder temperatures Steller's Eiders (*Polysticta stelleri*) not only increased time spent foraging but also adjusted how they forage, by reducing the frequency of costly dives. Although they are normally diurnal foragers (Goudie et al. 2000), eiders, particularly ones wintering at high latitudes, have been known to feed at night (Systad et al. 2000; F.R. Merkel and A. Mosbech, personal communication). Therefore, feeding in either day or night may

enable eiders to maintain a constant level of reserves despite conditions of winter (i.e., ambient temperature and shortening day length).

Disturbance due to hunting activities also can have negative effects on body condition in waterfowl (Gaston 1991). Hunting disturbance can prevent birds from feeding by displacing them from foraging areas and cause them to expend energy to escape hunters. Common eiders are considered to be particularly sensitive to hunting disturbance (Bell and Owen 1990). In Greenland, hunting disturbance and photoperiod were highly correlated (Fig. 2; unpublished data), because winter outdoor activities are usually limited to daylight hours at northern latitudes. If lipid levels were strongly influenced by either of these factors, lipids should peak in early and mid winter, then decline throughout late winter and spring as day length changes. This pattern was observed in juveniles, particularly among males (Table 1). However, changes to hunting regulation during the years of this study suggest that photoperiod, rather than hunting intensity itself, was the influencing factor. Hunting intensity declined dramatically in the winter of 2002 compared to 2000 and 2001 (Fig. 2b), but

there was no corresponding change in eider body condition (Table 1).

In general, lipid dynamics of eiders wintering in Greenland were not strongly influenced by current or historical ambient temperatures, hunting disturbance, or photoperiod. The only significant relationship found was between photoperiod and lipid levels of juvenile males. Eiders may have adjusted their behavior to overcome any negative effects of environmental conditions on their energetics. It is also possible that patterns were not detected because of the monthly temporal scale over which eiders were collected, and that variation in energetic reserves may have been occurring at a finer time scale.

Northern populations

Adult eiders collected in Greenland carried larger mean lipid reserves (females 205 g, males 221 g) than eiders wintering at more southerly, temperate regions (females ~160 g, males ~170 g, Scotland, Milne 1976; females 175 g, Maine, Korschgen 1977; males 17–170 g, Québec, Guillemette et al. 1992). Parker and Holm (1990), who also studied a northern population of eiders in Svalbard, found that nonbreeding females carried substantial lipid reserves (241 g). Therefore, our findings support the theory that the threat of prolonged nutritional shortages is higher at more northerly latitudes and that eiders respond to this by storing more energy reserves.

Despite the northerly latitude of the Greenland coast, the low variability of reserve levels (despite some differences in age classes and year) suggests a more constant food resources availability compared to other waterfowl species in winter. This would be expected because Northern Eiders feed on benthic, immobile prey found in shallow water, and in a region largely absent of sea ice (Boertmann et al. 2004). Their foraging strategies and risk sensitivity may be in contrast with other waterfowl species in which vegetative and/or invertebrate prey may be more ephemeral in winter (Lovvold 1994). We conclude that the discrepancies we detected from the typical waterfowl patterns emphasize the need to examine other bird populations wintering in a variety of environments to help determine what factors may cause deviations from the typical waterfowl pattern.

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